Mem. Qd Mus. (1971) **16**(1): 1–18.

MORPHOLOGY AND VARIATION OF THE CHEEK TEETH IN *MACROPUS GIGANTEUS* SHAW AND *MACROPUS AGILIS* (GOULD)

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ABSTRACT

The cheek teeth in the Grey Kangaroo, *Macropus giganteus* Shaw, and the Sandy Wallaby, *M. agilis* (Gould) have been described and the variation investigated. The results generally indicate considerably less variation in molar teeth and in the deciduous, molariform premolar, DP^3_3, than in the remaining premolar teeth in the series, P_2 and especially P^3_3. In the cheek teeth, sexual dimorphism in metrical features is shown to be a factor warranting consideration in macropodid species.

The present investigation was initiated to provide adequate information on cheek teeth variation in large, sexed samples of selected, extant macropodids. The necessity for this type of study has become increasingly apparent in connection with investigations on extinct macropodid faunas. To facilitate an assessment of possible size and morphological variation and the determination of species limits associated with this largely Upper Cainozoic taxonomic research, an accurate knowledge of variation present in extant species is of paramount importance.

The study has been restricted to cheek teeth because these are relatively abundant and well preserved elements in the fossil deposits and, for the most part, fossil species are defined by the morphology of their cheek teeth. These skeletal elements are frequently in sufficiently large numbers to allow meaningful statistical analyses and comparisons to be undertaken (Bartholomai, 1967).

The species *M. giganteus* and *M. agilis* have been selected for study for a number of reasons. Most important is the existence of closely related material in Pleistocene deposits, particularly in the fluviatile deposits of the Darling Downs area, southeastern Queensland, and the results will be of direct value for comparison in this regard. Large, sexed samples

of *M. giganteus* and *M. agilis* are available, mainly as a result of investigations on living macropodids currently being undertaken by the Queensland Department of Primary Industries. Samples considered have been collected from restricted areas, *M. giganteus* from the environs of Warwick, southeastern Queensland, and *M. agilis* from the Townsville area, mid-eastern Queensland. Use of these has obviated the necessity to consider possible geographical variation. Results are thus of greater value for use in comparisons with geographically and stratigraphically restricted fossil samples. Finally, the selection has allowed an assessment of sexual dimorphism to be undertaken within the 'kangaroo' and 'wallaby' groups within the Family Macropodidae.

Limited information has previously been available on the subject (Tedford, 1967), but for the most part the statistical results were based on small, geographically diversified samples, reducing their value for the purposes intended.

Primary data sheets have been lodged in the Library of the Queensland Museum, and the specimens from which data were derived are being progressively transferred and registered into the neontological collections of the Queensland Museum. All measurements throughout are in millimetres.

The author wishes to express his appreciation to Dr T. H. Kirkpatrick of the Queensland Department of Primary Industries, for making available for study the skull remains here considered.

CHEEK TEETH IN *MACROPUS GIGANTEUS* SHAW, 1790

P^2 relatively elongate, broader posteriorly than anteriorly, markedly constricted mesially in occlusal view. Paracone and metacone well developed, high, connected by secant ridges ascending into mesial constriction, giving longitudinal crest a well defined bifid appearance in lateral view; slight cuspule frequently present towards limit of anterior metacone ridge, accompanied by slight, vertical labial and lingual ridges; protocone low, moderately well defined, with low anterior ridge usually curving labially to unite with anterior ridge from paracone at anterior limit of crown; posterior ridge from protocone less well defined, ascending at lingual limit of mesial crown constriction, usually uniting with low, broad ridge which descends from postero-lingual portion of paracone; protocone ridge occasionally unites directly at that point; hypocone relatively strongly developed, well defined, occasionally connected labially by weak ridge to base of metacone; connecting ridge more frequently ascends from anterior hypocone ridge which curves to postero-lingual base of paracone; posterior ridge from hypocone curves labially to unite with posterior ridge from metacone at posterior margin of crown. Lingual basin irregular, divided into anterior, mesial, and posterior pockets; occasionally additional minor pocket developed

mesially. Slight cuspule or ridge sometimes present at antero-lingual base of hypocone. Small cuspule occasionally present labiad to and below metacone; where absent, cuspule frequently replaced with slight ridge to metacone.

DP^3 molariform, subrectangular in basal outline, slightly constricted across median valley; lophs relative high, but metaloph higher than protoloph, bowed anteriorly, with metaloph broader than protoloph. Anterior cingulum moderately low, usually broad, short, ascending lingually, with only slight indication of presence of forelink usually seen near axis of crown. Ridge usually ascends from paracone to unite with labial limit of cingulum; occasionally anterior paracone ridge descends within labial cingular limit. Midlink strong, moderately high, curving postero-labially from protocone, uniting with short ridge from point on metaloph slightly linguad to axis of crown; junction frequently puckered. Median valley V-shaped, occasionally more broadly U-shaped in lingual moiety; slight ridges acsend towards base of valley from paracone and metacone; lingually, valley occasionally with low, broad ridge transverse to crown axis. Ridge from hypocone strong, ascending posteriorly to near postero-labial base of crown; posterior ridge from metacone weak. Slight fossette developed above axis of crown; slight vertical groove often present on hypocone ridge, close to hypocone.

P^3 comparatively small, subtriangular in basal outline being broader posteriorly than anteriorly, with slight mesial constriction lingually. Paracone and metacone well developed, relatively high, connected by secant ridges which normally ascend into mesial cleft, giving crest a marked bifid appearance in lateral view; posterior portion frequently better developed than anterior; subsidiary cuspule occasionally present, associated with a pair of vertical labial and lingual ridges, towards limit of anterior metacone ridge; this cuspule rarely better developed; slight pockets also very rarely developed on both anterior and posterior moieties of crests. Anterior ridge from paracone ascends towards base of crown, associated with low ridge around anterior margin where this developed, while posterior ridge from metacone curves lingually to below posterior base of crown. Hypocone less well defined than other cusps, usually connected labially to base of metacone by relatively strong ridge; where this ridge absent, base of metacone connected to anterior ridge from hypocone which ascends into lingual constriction of crown; posterior ridge from hypocone curves labially to below posterior margin of crown. Low, variable ridge developed basally, postero-lingual to paracone. Slight posterior fossette frequently present, but lingual basin largely undeveloped.

$M^1 < M^2 < M^3 < M^4$; molars subrhomboidal in basal outline, slightly constricted across median valley; lophs relatively high, bowed anteriorly, frequently puckered at unworn crest; metaloph broader than protoloph in M^1 and M^2, often approximately equal in M^3, and narrower in M^4; metaloph higher than protoloph. Anterior cingulum relatively low, moderately broad, short, ascending lingually, with forelink well developed, frequently very strong, linguad to axis of crown. Slight but variable ridge usually ascends from paracone to unite with labial limit of cingulum; occasionally ridge may disappear before reaching base of protoloph. Slight, vertical accessory ridges sometimes present on anterior surface

of protoloph. Midlink strong, moderately high, curving postero-labially from protocone, uniting with short ridge from point on metaloph slightly linguad to axis of crown; junction frequently puckered. Median valley V-shaped, occasionally more broadly U-shaped in lingual moiety; ridges ascending into valley from paracone and metacone usually poorly developed, especially that from metacone; lingual base of valley occasionally with low, broad ridge transverse to crown axis; lingual margin of median valley rarely with low ridge. Ridge from hypocone strong, ascending postero-labially to above postero-labial base of crown; posterior ridge from metacone weak. Slight fossette developed above axis of crown, while slight vertical groove often present on hypocone ridge, close to hypocone.

P_2 relatively small, subtriangular in basal outline, broader posteriorly than anteriorly, slightly constricted mesially in occlusal view. Longitudinal crest usually markedly bifid in lateral view, comprising secant ridges descending posteriorly from anterior cuspid and slightly curving lingually from postero-labial cuspid; occasionally additional cuspule present at anterior limit of posterior moiety of crest, this rarely elevated to produce near trenchent crest; cuspule associated with variable set of vertical labial and lingual ridges. Anterior ridge from anterior cuspid descends slightly lingually to variable but sometimes well elevated cuspule above base of crown; basal swellings associated with cuspule better developed lingually, with small basal tubercle frequently present postero-lingual to anterior cuspid. Postero-lingual cuspid well defined, high, with strong ridge descending labially to posterior cuspid of crest; anterior ridge from postero-lingual cuspid descends mesially to curve labially and unite with base of crest at position of cleft, defining relatively deep, posterior basin; slight variable ridges frequently present into basin. Occasionally small basal tubercle developed antero-lingual to internal cuspid.

DP_3 molariform, subtriangular in basal outline, moderately constricted across talonid basin, with lophids relatively high, strongly convex posteriorly. Hypolophid much broader than protolophid. Trigonid basin relatively narrow, its length being less than distance between lophids, with lingual portion near planar but with basin strongly descending labially. Forelink moderately strong, relatively low, descending slightly lingually from protoconid then anteriorly to antero-labial margin of high anterior cingulum. Midlink high, strong, descending antero-lingually from hypoconid and curving anteriorly, frequently abruptly, uniting with moderately well defined ridge from protoconid above talonid basin; junction often plicate; midlink crosses talonid slightly labiad to axis of crown. Talonid basin near planar and V-shaped lingually somewhat descending and U-shaped labially; labial moiety occasionally with slight, broad transverse ridge. Posterior surface of hypolophid generally convex but usually more angular postero-lingually; slight groove descends postero-lingually from position mesiad to hypocone.

P_3 relatively small, subtriangular to subovate in basal outline, usually broader posteriorly and slightly constricted mesially. Anterior margin of crown near vertical. Anterior cuspid with trenchent ridge usually descending to unite with descending ridge from postero-labial cuspid slightly posterior to mid-point of crown; crest usually bifid in lateral view, but

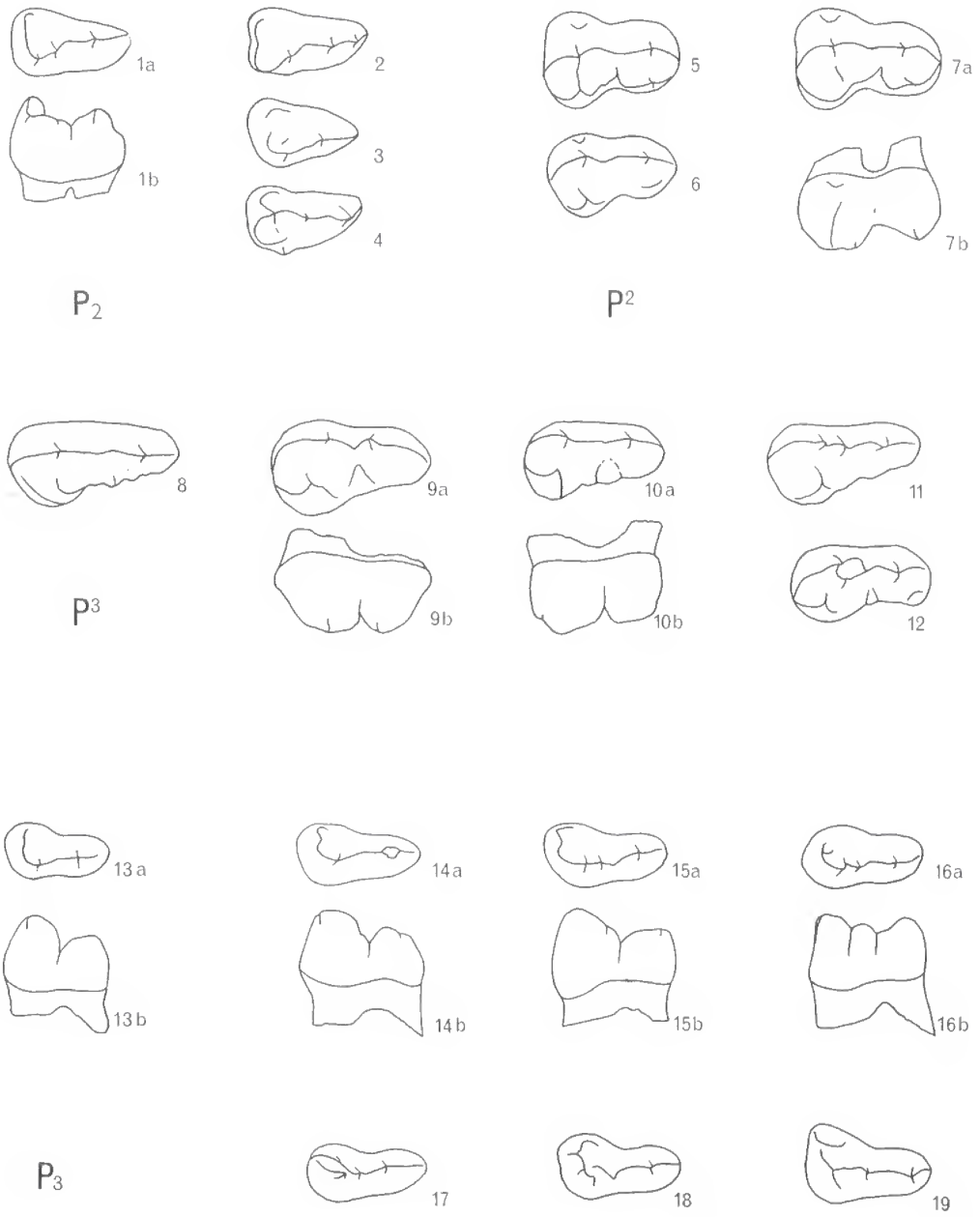

FIG. 1: Some variation in the morphology of deciduous and permanent premolars in the Grey Kangaroo, *Macropus giganteus* Shaw. P_2: 1, J20368; 2, J20847; 3, J20901; 4, J20983. P^2: 5, J20847; 6, J20901; 7, J20368. P^3: 8, J20388; 9, J20390; 10, J20396; 11, J20389; 12, J20397. P_3: 13, J20397; 14, J20385; 15, J20388; 16, J20398; 17, J20384; 18, J20389; 19, J20390. a = occlusal view; b = lateral view. All specimens in the Queensland Museum.

occasional low cuspid developed at base of cleft, associated with set of vertical labial and lingual ridges; this cuspule rarely better developed to give crest a trifid appearance in lateral view; posterior ridge from anterior cuspid occasionally with pocket developed along occlusal surface. Posterior ridge from postero-labial cuspid curves lingually, usually to unite with high, poorly defined postero-lingual cuspid, but occasionally descending to postero-lingual base of crown.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly constricted across talonid basin; lophids relatively high, bowed posteriorly, frequently puckered at unworn crest; hypolophid broader than protolophid in M_1 and M_2, often approximately equal in M_3 and narrower in M_4; hypolophid higher than protolophid. Anterior cingulum relatively high, usually indented anteriorly, moderately broad, its length approximately equalling distance between lophids; cingulum descends slightly lingually and markedly labially. Forelink high, strong, descending antero-lingually from protoconid then anteriorly or slightly labially to point labiad to mid-point of cingulum. Trigonid basin better developed lingually than labially, with antero-labial fossette normally present in labial moiety. Anterior and posterior ridges from metaconid poorly developed. Midlink strong, relatively high, descending antero-lingually from hypoconid then anteriorly above talonid basin to unite with very short ridge from below or slightly linguad to protoconid; junction often puckered. Labial moiety of talonid V-shaped, lingual portion U-shaped; occasional, low, transverse ridge present in base of lingual portion of basin; talonid slopes labially and lingually from midlink. Anterior ridge from entoconid poorly developed. Posterior surface of hypolophid with moderately deep, broad diagonal groove from near hypoconid to near postero-lingual base of crown.

CHEEK TEETH IN *MACROPUS AGILIS* (GOULD, 1842)

P^2 elongate, slightly broader posteriorly than anteriorly, slightly convex labially and concave lingually in occlusal view. Paracone and metacone well developed, high, connected by high secant longitudinal crest; crest straight or slightly concave labially in occlusal view, transected about one-half way between cusps by well defined set of vertical labial and lingual ridges, with production of cuspule at crest. Very weak second set of ridges sometimes present close to metacone. Occasionally labial ridge from cuspule bifurcates basally. Anterior and posterior ridges from paracone and metacone act as continuation of longitudinal crest, ascending and curving lingually towards base of crown. Protocone low, poorly defined; anterior ridge from protocone curves labially below base of crown as extension of lingual cingulum; posterior ridge from protocone forms low lingual cingulum; cingulum slightly sinuous in lateral view; lingual basin shallow, crossed by low transverse ridges from cuspules on cingulum to base of longitudinal crest; hypocone better defined but low, with its anterior ridge contributing to lingual cingulum; posterior hypocone ridge curves labially below base of crown to unite with posterior metacone ridge; labially, low

ridge connects hypocone to lingual ridge ascending from metacone. Postero-lingual fossette shallow.

DP^3 molariform, subrectangular to subtriangular in occlusal view, slightly constricted across median valley; lophs relatively low, but with metaloph higher than protoloph, bowed anteriorly with metaloph considerably broader than protoloph. Anterior cingulum relatively low and narrow, short, ascending lingually with no indication of presence of forelink; ridge ascends from paracone to limit of cingulum forming moderately high secant area in functional continuity with longitudinal crest of P^2. Midlink relatively strong, low, curving postero-labially from protocone to metaloph, near axis of crown; slight contribution to midlink from metaloph. Median valley V-shaped, occasionally more broadly

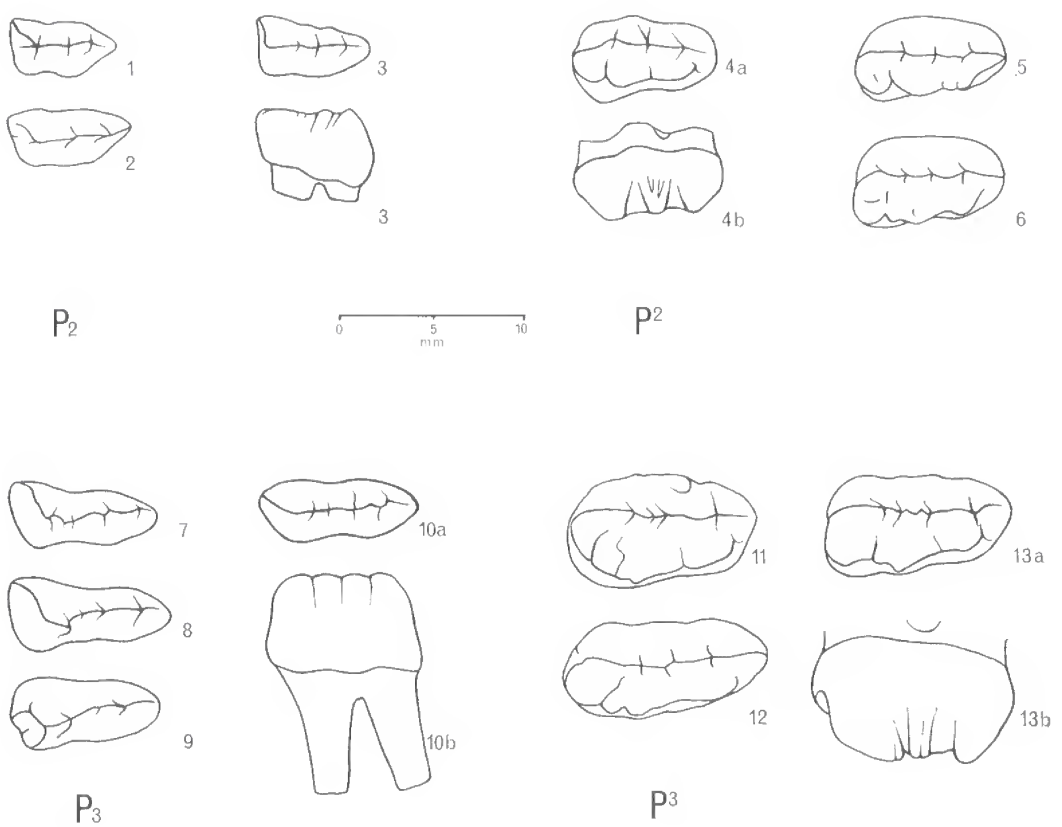

FIG. 2: Some variation in the morphology of deciduous and permanent premolars in the Sandy Wallaby, *Macropus agilis* (Gould). P_2: 1, J14813; 2, J14606; 3, J14678. P^2: 4, J14678; 5, J14813; 6, J14632. P_3: 7, J14597; 8, J14594; 9, J14579; 10, J14622. P^3: 11, J14594; 12, J14602; 13, J14622. a = occlusal view; b = lateral view. All specimens in the Queensland Museum.

U-shaped in lingual moiety. Posterior ridge from paracone and anterior ridge from metacone curve into valley uniting to form accessory structure across labial moiety of valley. Posterior ridge from hypocone strong, curving across posterior surface of crown towards postero-lingual margin; posterior ridge from metacone weak; posterior fossette usually well defined.

P^3 relatively large, subovate to subtriangular in basal outline, being broader posteriorly than anteriorly; crown slightly convex labially, slightly concave lingually. Paracone and metacone well developed, high, connected by high secant longitudinal crest which is straight or slightly concave labially; crest normally transected by two sets of vertical labial and lingual ridges, with set near mid-point of crest usually best developed. Occasionally, third set of very slight ridges present near metacone; slight cuspules present along crest, associated with transecting ridges. Anterior and posterior ridges from paracone and metacone respectively ascend towards base of crown, with that from metacone curving lingually. Protocone poorly defined, low, with anterior ridge disappearing below antero-lingual base of crown. Posterior ridge from protocone forms low lingual cingulum; cingulum normally slightly sinuous in occlusal and lateral views. Lingual basin shallow, usually slightly broader posteriorly, crossed occasionally by slight ridges to base of longitudinal crest; occasionally transverse ridge close to hypocone stronger developed. Hypocone much stronger than protocone, moderately high, with anterior ridge contributing to lingual cingulum; posterior ridge curves labially to unite with posterior ridge from metacone; labial ridge from hypocone relatively strong, uniting with ridge from metacone at base of longitudinal crest. Postero-lingual fossette well defined.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley; lophs relatively low, bowed anteriorly, frequently puckered at unworn loph crests; metaloph broader than protoloph in M^1 and M^2, often approximately equal in M^3, and narrower in M^4; metaloph higher than protoloph. Anterior cingulum low, broad, short, ascending lingually, with forelink normally absent; occasionally low ridge crosses as forelink from base of protoloph to cingulum approximately below axis of crown, but this never very strong. Strong ridge ascends from paracone to labial limit of cingulum. Midlink strong, low, curving postero-labially from protocone, uniting with short ridge from near mid-point of metaloph. Median valley usually V-shaped; ridges ascending into valley from paracone and metacone usually weak, but occasionally these unite across labial moiety providing subsidiary link. Posterior ridge from hypocone strong, ascending labially to point slightly labiad to axis of crown above base of crown; posterior ridge from metacone somewhat weaker, curving lingually to unite with hypocone ridge, forming margin to well defined posterior fossette.

P_2 relatively elongate and comparatively large, subovate to subtriangular in basal outline, usually slightly broader posteriorly than anteriorly; frequently crown slightly constricted at posterior one-third, but occasionally labial surface convex and lingual concave. Longitudinal crest well defined, high, secant, with anterior and posterior cuspids

well defined; crest usually transected mesially by a single set of vertical or near vertical labial and lingual ridges but occasionally a less well developed set may be present close to posterior cuspid; cuspules developed at crest associated with transecting ridges. Posterior extension of crest curves lingually before descending to postero-lingual base of crown; occasionally slight posterior ridge from posterior cuspid of crest also present. Base of crown rarely tumid, particularly labially.

DP_3 molariform, subtriangular in basal outline, very slightly constricted across talonid basin; lophids relatively low, bowed posteriorly, with hypolophid broader than protolophid. Trigonid basin relatively narrow, its length being less than distance between lophids, with lingual portion near planar but with basin strongly descending labially. Forelink low, strong, descending labially from protoconid to point on anterior cingulum labiad to axis of crown; anterior cingulum moderately low. Metaconid with moderately strong ridge descending anteriorly into trigonid and occasionally to lingual limit of cingulum. Midlink strong, low, descending anteriorly from hypocone to unite with short ridge from protolophid somewhat labiad to axis of crown. Talonid basin near planar, V-shaped. Postero-lingual margin of crown usually somewhat angular.

P_3 relatively large, elongate, subovate to subtriangular in basal outline, usually slightly broader posteriorly than anteriorly; frequently crown slightly to moderately constricted at posterior one-third. Longitudinal crest well defined, high, secant, with anterior and posterior cuspids well defined; crest normally transected by two sets of vertical or near vertical labial and lingual ridges of which the anterior set are better developed; cuspules are present at crest associated with transecting ridges; rarely crest puckered in unworn teeth. Posterior extension of crest slightly to strongly developed, either gently curving lingually to descend to base of crown or verging to abruptly curving lingually before descending. Base of crown rarely tumid labially.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, very slightly constricted across talonid basin; lophids relatively low, bowed posteriorly, rarely puckered at unworn crest; hypolophid broader than protolophid in M_1 and M_2, often approximately equal in M_3, and narrower in M_4; hypolophid higher than protolophid. Anterior cingulum moderately low, relatively narrow, its length being slightly less than distance between lophids. Trigonid basin with lingual portion near planar, but markedly descending in labial portion. Forelink usually relatively low, strong, curving antero-lingually from protoconid to point on cingulum slightly labiad to axis of crown; rarely slight suggestion of accessory link present towards base of protolophid. Anterior ridge from metaconid usually very poorly developed or absent. Midlink relatively low, strong, descending from hypoconid to unite with slight ridge from protolophid labiad to axis of crown; junction occasionally incomplete or puckered. Labial moiety of talonid basin V-shaped but lingual portion frequently more broadly U-shaped. Rarely low fold present towards base of hypolophid close to midlink. Posterior surface of hypolophid normally gently convex.

TABLE 1

SUMMARY OF MEASUREMENTS FOR COMPLETE SAMPLE OF *Macropus giganteus* SHAW

Character	Maxillae					Mandibles				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
P^2_2 length	55	6.3– 7.8	7.0	0.2893	4.13	50	5.4– 7.2	6.5	0.3502	5.39
maximum breadth ..	55	4.0– 5.6	4.8	0.2963	6.17	49	3.1– 3.9	3.5	0.1958	5.59
DP^3_3 length	65	7.5– 0.1	8.5	0.3801	4.47	50	7.9– 9.7	8.7	0.3382	3.89
breadth protoloph(-id) ..	65	5.7– 7.2	6.5	0.3799	5.84	48	4.2– 5.2	4.6	0.2208	4.80
P^3_3 length	42	6.1– 8.2	7.3	0.4949	6.78	40	5.1– 7.0	6.1	0.4629	7.59
maximum breadth ..	41	3.1– 4.6	3.9	0.3599	9.23	40	2.3– 3.7	3.1	0.3522	11.36
M^1_1 length	134	8.0–11.0	9.9	0.5362	5.42	100	8.6–11.7	10.2	0.5391	5.29
breadth protoloph(-id) ..	134	6.6– 8.7	7.5	0.4248	5.66	99	4.7– 6.8	5.9	0.3185	5.40
M^2_2 length	130	9.6–13.0	11.1	0.6506	5.86	106	8.9–13.2	11.7	0.7081	6.05
breadth protoloph(-id) ..	130	7.4– 9.7	8.4	0.4513	5.37	109	5.7– 7.9	7.0	0.3947	5.64
M^3_3 length	92	10.3–14.0	11.9	0.6239	5.24	77	11.4–14.3	12.6	0.6479	5.14
breadth protoloph(-id) ..	92	8.1–10.1	9.0	0.4876	5.42	83	6.6– 8.5	7.5	0.4327	5.77
M^4_4 length	59	11.2–14.0	12.6	0.6113	4.85	57	11.8–14.9	13.2	0.7833	5.93
breadth protoloph(-id) ..	58	8.4–11.1	9.4	0.5289	5.62	59	6.7– 8.7	7.7	0.5219	6.78

TABLE 2

SUMMARY OF MEASUREMENTS FOR COMPLETE SAMPLE OF *Macropus agilis* (GOULD)

Character	Maxillae					Mandibles				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
P_2^2 length	28	6.5– 7.8	7.1	0.3442	4.85	29	5.4– 6.8	6.0	0.3813	6.36
maximum breadth ..	15	3.8– 4.6	4.2	0.2170	5.17	29	2.5– 5.3	2.9	0.2179	7.51
DP_3^3 length	29	6.4– 7.7	7.0	0.3422	4.89	30	5.4– 7.6	6.5	0.4223	6.50
breadth protoloph(-id) ..	27	4.9– 5.5	5.2	0.1628	3.13	29	3.6– 4.5	3.9	0.2205	5.65
P_3^3 length	122	8.3–10.5	9.2	0.4496	4.89	133	6.8– 9.1	7.8	0.4272	5.48
maximum breadth ..	115	4.0– 5.9	4.8	0.3497	7.29	131	2.3– 4.0	3.1	0.3163	10.20
M_1^1 length	118	6.4– 8.5	7.5	0.4084	5.45	111	6.3– 8.3	7.3	0.4789	6.56
breadth protoloph(-id)..	125	5.6– 6.9	6.3	0.2655	4.21	135	4.0– 5.7	4.9	0.2665	5.44
M_2^2 length	138	7.6– 9.9	8.9	0.4923	5.53	139	7.5–10.0	8.8	0.5009	5.69
breadth protoloph(-id) ..	153	6.3– 8.3	7.2	0.3335	4.63	149	5.2– 6.5	5.8	0.2641	4.55
M_3^3 length	134	8.8–11.1	10.0	0.4866	4.87	128	8.6–10.0	10.0	0.4894	4.89
breadth protoloph(-id) ..	133	7.0– 8.9	7.9	0.3707	4.69	132	5.5– 7.5	6.4	0.3491	5.45
M_4^4 length	80	9.2–11.8	10.6	0.04660	4.40	79	9.5–11.7	10.8	0.5164	4.78
breadth protoloph(-id) ..	69	7.2– 9.2	8.1	0.4039	4.99	80	5.8– 7.7	6.6	0.3279	5.42

TABLE 3

SUMMARY OF MEASUREMENTS FOR SEXED SAMPLES OF *Macropus giganteus* SHAW

Character	Male Sample					Female Sample				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
P^2 length	22	6.5– 7.7	7.0	0.2802	4.00	33	6.3– 7.8	7.0	0.2973	4.25
maximum breadth	22	4.6– 5.6	5.0	0.2213	4.43	33	4.0– 5.6	4.7	0.3051	6.49
DP^3 Length	26	8.0– 9.1	8.6	0.3440	4.00	39	7.5– 9.0	8.3	0.3814	4.60
breadth protoloph	26	5.9– 7.2	6.6	0.4014	6.08	39	5.7– 6.7	6.2	0.2377	3.83
P^3 length	16	6.5– 8.2	7.5	0.5170	6.89	26	6.1– 8.1	7.2	0.4698	6.53
maximum breadth	16	3.4– 4.6	4.1	0.4242	10.35	25	3.1– 4.6	3.8	0.2805	7.38
M^1 length	55	9.1–11.0	10.1	0.4107	4.07	79	8.0–10.5	9.7	0.5180	5.34
breadth protoloph	55	6.7– 8.7	7.8	0.4291	5.50	79	6.6– 8.0	7.4	0.3116	4.21
M^2 length	48	10.0–13.0	11.4	0.6855	6.01	82	9.6–12.1	10.9	0.5748	5.27
breadth protoloph	47	7.9– 9.7	8.8	0.4310	4.90	83	7.4– 9.0	8.3	0.3514	4.23
M^3 length	34	11.6–14.0	12.3	0.5626	4.57	58	10.3–13.6	11.8	0.5557	4.71
breadth protoloph	34	8.5–10.1	9.4	0.4022	4.28	58	8.1– 9.7	8.7	0.3811	4.38
M^4 length	22	11.9–14.0	13.0	0.5131	3.95	37	11.2–13.4	12.3	0.4717	3.83
breadth protoloph	22	9.1–11.1	9.9	0.4196	4.24	36	8.4– 9.9	9.2	0.3817	4.15
P_2 length	18	5.9– 7.2	6.6	0–3418	5.18	32	5.4– 6.9	6.5	0.3198	4.92
maximum breadth	18	3.3– 3.9	3.6	0.1984	5.51	31	3.1– 3.8	3.5	0.1905	5.44
DP_3 length	18	8.3– 9.7	8.9	0.3298	3.71	32	7.9– 9.1	8.6	0.2961	3.44
breadth protolophid	17	4.2– 5.2	4.7	0.2511	5.34	31	4.2– 4.9	4.6	0.1732	3.77
P_3 length	18	5.6– 7.0	6.3	0.4517	7.16	22	5.1– 6.7	5.9	0.3969	6.73
maximum breadth	18	2.6– 3.7	3.2	0.3316	10.36	22	2.3– 3.7	3.0	0.3358	11.19
M_1 length	40	9.7–11.7	10.5	0.4346	4.14	60	8.6–11.2	10.0	0.5471	5.47
breadth protolophid	38	5.6– 6.8	6.1	0.2854	4.68	61	4.7– 6.4	5.8	0.2692	4.64
M_2 length	40	11.2–13.2	12.0	0.5088	4.24	66	8.9–13.0	11.4	0.7041	6.18
breadth protolophid	41	6.6– 7.9	7.3	0.3227	4.42	68	5.7– 7.6	6.8	0.3394	4.99
M_3 length	29	12.2–14.3	13.0	0.5027	3.87	48	11.4–14.0	12.3	0.5652	4.60
breadth protolophid	32	7.4– 8.5	7.9	0.2769	3.51	51	6.6– 8.1	7.3	0.3831	5.25
M_4 length	21	12.6–14.9	14.0	0.5692	4.07	36	11.8–14.0	12.8	0.5484	4.28
breadth protolophid	21	7.5– 8.7	8.2	0.3170	3.87	38	6.7– 8.3	7.5	0.3875	5.17

TABLE 4

SUMMARY OF MEASUREMENTS FOR SEXED SAMPLES OF *Macropus agilis* (GOULD)

Character	Male Sample					Female Sample				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
P^2 length	18	6.8– 7.8	7.2	0.3067	4.62	10	6.5– 7.4	6.9	0.3179	4.61
maximum breadth	11	3.8– 4.6	4.2	0.2408	5.73	4	4.0– 4.4	4.2	0.4000	9.52
DP^3 length	19	6.6– 7.7	7.1	0.3511	4.95	10	6.4– 7.3	6.9	0.2600	3.77
breadth protoloph	18	4.9– 5.5	5.2	0.3307	6.36	9	4.9– 5.3	5.1	0.1414	2.77
P^3 length	61	8.6–10.5	9.3	0.4659	5.01	61	8.3–10.0	9.2	0.4260	4.63
maximum breadth	56	4.1– 5.9	4.9	0.3535	7.21	59	4.0– 5.6	4.8	0.3546	7.39
M^1 length	63	6.6– 8.5	7.7	0.3570	4.64	55	6.4– 8.5	7.4	0.4048	5.47
breadth protoloph	67	5.8– 6.9	6.3	0.7435	11.80	58	5.6– 6.8	6.1	0.8056	13.21
M^2 length	71	7.6– 9.9	9.1	0.4406	4.84	67	7.8– 9.6	8.6	0.4296	5.00
breadth protoloph	78	6.5– 8.3	7.3	0.3114	4.27	75	6.3– 7.7	7.1	0.3029	4.27
M^3 length	66	9.1–11.1	10.2	0.4288	4.20	68	8.8–10.9	9.8	0.4593	4.69
breadth protoloph	66	7.3– 8.9	8.0	0.3327	4.16	67	7.0– 8.4	7.7	0.3283	4.26
M^4 length	36	10.2–11.8	10.8	0.3633	3.36	44	9.2–11.5	10.4	0.4560	4.38
breadth protoloph	27	7.5– 9.2	8.4	0.3597	4.28	42	7.2– 8.7	8.0	0.3334	4.56
P_2 length	19	5.4– 6.8	6.1	0.3770	6.18	10	5.4– 6.7	6.0	0.3887	6.48
maximum breadth	19	2.6– 3.3	3.0	0.2092	6.97	10	2.5– 3.2	2.9	0.2236	7.71
DP_3 length	20	5.4– 7.6	6.5	0.4656	7.16	10	5.9– 7.1	6.4	0.3214	5.02
breadth protolophid	19	3.6– 4.5	4.0	0.2271	5.68	10	3.6– 4.0	3.8	0.1493	3.93
P_3 length	65	6.8– 9.1	7.9	0.4756	6.02	68	7.0– 8.2	7.7	0.3212	4.17
maximum breadth	64	2.6– 4.0	3.2	0.2969	9.28	67	2.3– 3.9	3.0	0.2920	9.73
M_1 length	64	6.4– 8.3	7.5	0.4460	5.95	47	6.3– 8.0	7.2	0.4795	6.66
breadth protophid	73	4.5– 5.7	5.0	0.2229	4.46	62	4.0– 5.2	4.8	0.2539	5.29
M_2 length	76	7.8–10.0	8.9	0.4549	5.11	63	7.4– 9.5	8.6	0.4738	5.51
breadth protolophid	79	5.3– 6.5	5.9	0.2709	4.59	70	5.2– 6.2	5.7	0.2362	4.14
M_3 length	62	9.1–10.9	10.2	0.3383	3.32	66	8.6–10.9	9.7	0.4865	5.02
breadth protolophid	66	5.9– 7.5	6.6	0.3033	4.60	66	5.5– 7.1	6.3	0.3163	5.02
M_4 length	33	10.2–11.7	11.0	0.3630	3.30	46	9.5–11.1	10.3	0.4000	3.88
breadth protolophid	32	6.1– 7.7	6.8	0.3631	5.34	48	5.8– 6.9	6.5	0.2315	3.56

TABLE 5

COMPARISON OF SEXED SAMPLES OF *Macropus giganteus* BY STUDENT'S t-TEST

Maxillae			Mandibles		
Character	t	P	Character	t	P
P^2 length			P_2 length	3.27	0.001–0.01
maximum breadth	3.96	<0.001	maximum breadth	2.63	0.01–0.02
DP^3 length	3.34	<0.001	DP_3 length	3.64	<0.001
breadth protoloph	5.03	<0.001	breadth protolophid	1.62	0.1–0.2
P^3 length	1.93	0.05–0.1	P_3 length	3.67	<0.001
maximum breadth	2.72	0.001–0 01	maximum breadth	1.88	0.05–0.1
M^1 length	4.77	<0 001	M_1 length	4.84	<0 001
breadth protoloph	6.25	<0 001	breadth protolophid	4.88	<0 001
M^2 length	4.45	<0 001	M_2 length	4.69	<0 001
breadth protoloph	7.15	<0 001	breadth protolophid	7.58	<0 001
M^3 length	4.14	<0 001	M_3 length	5.51	<0 001
breadth protoloph	6 02	<0 001	breadth protolophid	7.68	<0 001
M^4 length	5.33	<0 001	M_4 length	7.85	<0 001
breadth protoloph	6.52	<0.001	breadth protolophid	7.07	<0.001

TABLE 6

COMPARISON OF SEXED SAMPLES OF *Macropus agilis* BY STUDENT'S t-TEST

Maxillae			Mandibles		
Character	t	P	Character	t	P
P^2 length	2.45	0.02–0.05	P_2 length	0.21	0.8–0.9
maximum breadth	—	—	maximum breadth	0.38	0.7–0.8
DP^3 length	1.58	0.1–0.2	DP_3 length	0.61	0.5–0 6
breadth protoloph	0.90	0.3–0.4	breadth protolophid	2.51	0.01–0 02
P^3 length	0.39	0.7–0.8	P_3 length	0.90	0.3–0.4
maximum breadth	0.48	0 6–0.7	maximum breadth	1.23	0.2–0.3
M^1 length	1.35	0.1–0.2	M_1 length	1.07	0.2–0.3
breadth protoloph	0.46	0 6–0.7	breadth protolophid	1.54	0.1–0.2
M^2 length	2.14	0.02-0.05	M_2 length	1.20	0.2–0.3
breadth protoloph	1.28	0.2–0 3	breadth protolophid	1.51	0.1–0.2
M^3 length	1.27	0 2–0.3	M_3 length	2.13	0.02–0.05
breadth protoloph	1.65	0.05–0.1	breadth protolophid	1.76	0.05–0.1
M^4 length	1.29	0.2–0.3	M_4 length	2.53	0.01–0.02
breadth protoloph	1.49	0.1–0.2	breadth protolophid	1.42	0.1–0.2

DISCUSSION

Early palaeontological investigations, such as those of Owen (1874) or De Vis (1895), which frequently present the best comparative discussions of the dentition in the subfamily Macropodinae, have tended to stress the value of the premolars in defining the species described. More recent investigations involving dentition also tend to emphasize the value of the morphology and size of the premolars in taxonomic considerations. In this connection, Tate (1948) has argued largely on the basis of the permanent premolar for the inclusion of the wallabies within the fossil genus *Protemnodon* Owen, a conclusion no longer tenable. In the present study, species are referred to *Macropus*, following Calaby (1966).

The emphasis on premolars has largely resulted from the greater interspecific variation usually exhibited by these teeth. The molars are normally adequately described but they are frequently considered to possess insufficient features showing significant interspecific differences to justify any great value being placed on them. Where fossil species have been defined on the morphology of their molar teeth, the importance of the work has often been reduced by inadequate knowledge of intraspecific variation both in the species being described or in the living species drawn upon for comparison.

In examining in detail the morphology and size of the cheek teeth in the living Grey Kangaroo, *Macropus giganteus*, and the Sandy Wallaby, *M. agilis*, the most obvious impression is that intraspecific variation is fairly consistently high in the deciduous and permanent premolars, P_2^2 and to a greater extent in P_3^3. Variation is present in the molars and may infrequently be more extreme in the deciduous molariform premolar and anterior molar, but in these the basic hypsobrachyodont condition (hypsodont of Bensley, 1903) is usually only slightly affected by accessory structures, and the differences are frequently only a matter of degree of development. Notwithstanding these considerations, P_2^2 and P_3^3 do exhibit marked interspecific variation and there appears to be every advantage in maintaining a measure of dependence upon the taxonomic value of the morphology of these teeth. It is believed, however, that as many features as possible of the remaining cheek teeth should also be considered conjointly, together with an assessment of the variation likely to be encountered in the teeth and other morphological characters in the species concerned.

Apart from purely morphological variation encountered in the cheek teeth (see figures 1 and 2) in *M. giganteus* and *M. agilis*, intraspecific size variation is considerable and this must be taken into account in any taxonomic assessment. The summaries of measurements provided for each species includes an evaluation of size variation in each sample as a whole as well as for individual sexed samples, treated as if each was drawn from a natural population. In these, variation as defined by the Coefficient of Variation, V, is calculated to be from 3.44–11.36 in *M. giganteus* and 2.77–13.21 in *M. agilis*. By far the bulk of values fall between 4.00–6.00 in each species.

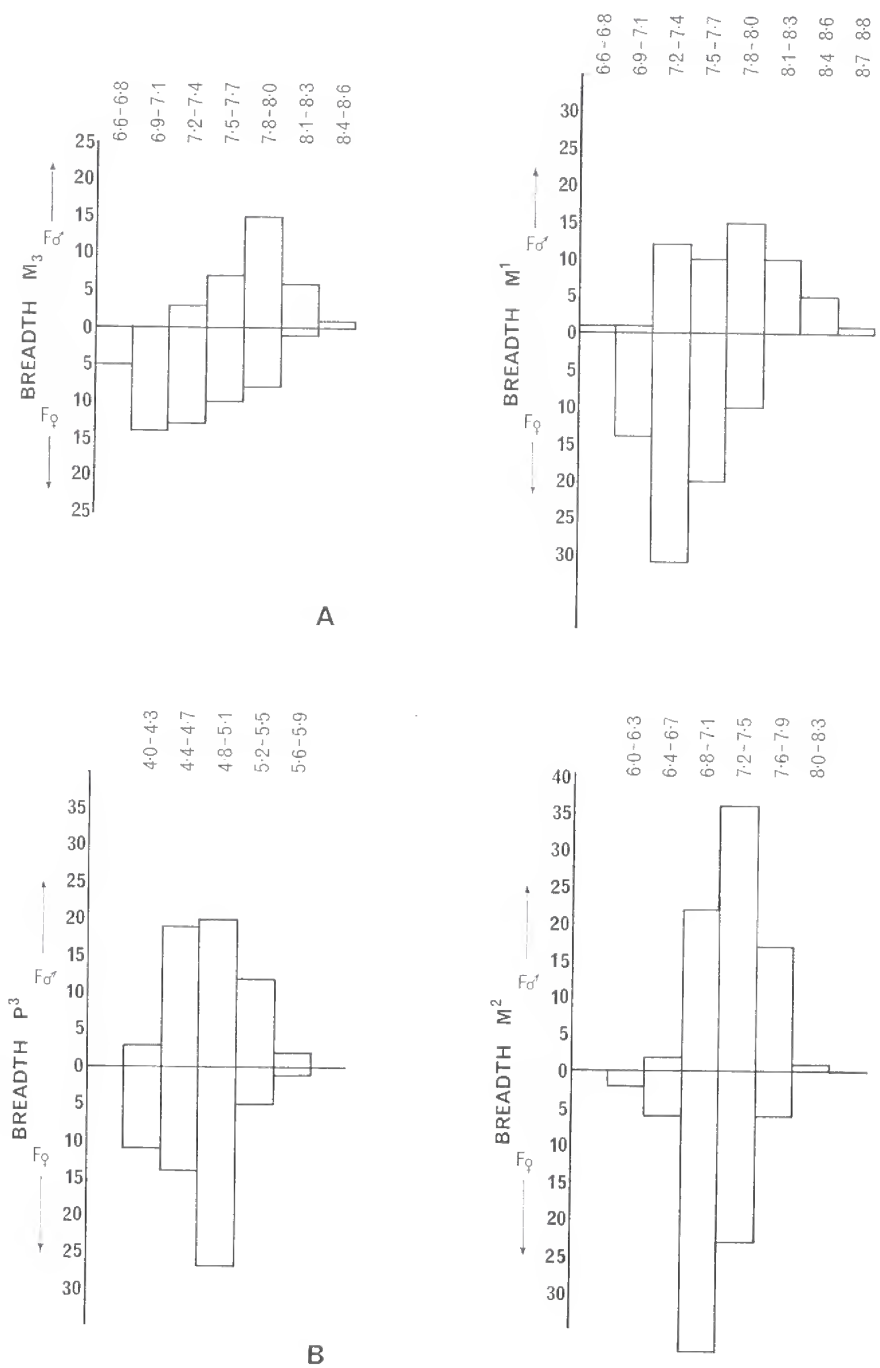

FIG. 3: Histograms for representative sexed samples of A, *Macropus giganteus* and B, *M. agilis*, illustrating the distribution of some dimensions in the cheek teeth.

Bartholomai (1967) has shown that in the fossil species *Troposodon minor* (Owen), V mostly falls between values of 4.00–7.00, but in this case the specimens comprising the sample were drawn from differing stratigraphic levels within the Upper Cainozoic deposits of the Darling Downs area and this fact most likely accounts for many of the slightly higher values than are present in the living macropodines. Studies on other Australian fossil macropodid samples by Merrilees (1965, 1967), Bartholomai (1970), and, in part, Tedford (1967) have yielded basically similar results for V to those in *T. minor*. Tedford's (1967) results for V in *M. ferragus*, however, are generally much higher than have so far been observed in recent or fossil macropodids suggesting mixing of this sample. Simpson *et al.* (1960) state that 'as a matter of observation, the great majority of them (values for V in mammals) lie between 4 and 10, and 5 and 6 are good average values.' Thus the bulk of the results for the living species of macropodines here considered conform with values of V for linear dimensions calculated for other mammal groups, and these are closely approximated by fossil results.

Values for V presented for some molar teeth dimensions in recent *M. canguru* in Tedford (1967) are generally higher than those for the present sample of *M. giganteus*. Differences apparent most probably relate to the fact that the material considered by Tedford was drawn from what is now believed to be two species (Kirsch and Poole, 1967), *M. fuliginosus* the Kangaroo Island and western mainland species of Grey Kangaroo and *M. giganteus*, the eastern Grey Kangaroo. Further, the material considered was collected from widely separated localities and some geographical variation may have been included.

An interesting situation exists between *M. giganteus* and *M. agilis* when the results of tables 5 and 6 are compared. These represent a comparison of means of the sexed samples for each species by use of Student's t test. Results for *M. agilis*, a member of the 'wallaby' group, approach significance at the 5% level in the lengths of P^2, M^2, and M_3 and at the 2% level in the protolophid breadth of DP_3 and the length of M_4. In *M. giganteus*, representing the 'kangaroo' group, the results are generally highly significant at the 0.1% level and only rarely are these not significant or do they only approach significance. Sexual dimorphism is therefore generally present in the Grey Kangaroo at least in the characters considered. This point could have significance where initial sorts of fossil material are being made utilizing frequency distributions. Bimodality in such distributions is thus likely within a single species but as can be seen in figure 3 the degree of separation of the modes is not necessarily excessive.

Kirkpatrick (1965) has shown that it is not uncommon for individuals of *M. giganteus* to possess a fifth molar tooth in the cheek teeth series. No evidence of the existence of M^5_5 was found in the sample used in the present study and results are not believed to have been complicated by this additional factor. While progression of the tooth row is evident in *M. agilis*, the P^3_3 are retained until late in life and identification of teeth is uncomplicated. In *M. giganteus*, however, there is actual loss of anterior teeth at an early age (Kirkpatrick, 1964), necessitating greater care in determination of molars after the permanent premolars have been ejected.

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